

GEOGRAPHIC VARIATION IN MORPHOLOGY OF FOUR SPECIES OF MIGRATORY RAPTORS

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ABSTRACT.—We studied geographic variation in morphology of four species of migratory raptor to test large-scale hypotheses of adaptive divergence in quantitative characters among migratory flyways. The Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*Accipiter cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), and American Kestrel (*Falco sparverius*) are co-distributed throughout North America. We examined patterns of morphological variation among raptors migrating along two western flyways, the Goshute Mountains of Nevada and Manzano Mountains of New Mexico, and one eastern flyway, Cape May Point in New Jersey. Although they were lower in mass, raptors from western flyways had significantly longer wings, longer tails or both, compared to conspecifics from an eastern flyway. It is significant that parallel variation in flight morphology occurs across four taxa that differ widely in taxonomic affinity, flight habits, size, and shape.

KEY WORDS: *Sharp-shinned Hawk*; *Accipiter striatus*; *Cooper's Hawk*; *Accipiter cooperii*; *Red-tailed Hawk*; *Buteo jamaicensis*; *American Kestrel*; *Falco sparverius*; *ecomorphology*; *migration*; *principal components analysis*.

VARIACIÓN GEOGRÁFICA EN LA MORFOLOGÍA DE CUATRO ESPECIES DE RAPACES MIGRATORIAS

RESUMEN.—Estudiamos la variación geográfica en la morfología de cuatro especies de rapaces migratorias para evaluar hipótesis a gran escala sobre la divergencia adaptativa en caracteres cuantitativos entre rutas migratorias. *Accipiter striatus*, *Accipiter cooperii*, *Buteo jamaicensis*, y *Falco sparverius* se encuentran co-distribuidos en América del Norte. Examinamos los patrones de variación morfológica entre las rapaces encontradas migrando a lo largo de dos rutas migratorias del oeste, las montañas Goshute de Nevada y las montañas Manzano de New Mexico, y una ruta del este, Cape May Point en New Jersey. Aunque presentaron menor masa corporal, las rapaces de las rutas del oeste tuvieron alas significativamente más largas, colas significativamente más largas, o ambas, comparadas con aves coespecíficas de la ruta del este. Es significativo que exista variación paralela en la morfología del vuelo en cuatro taxa que difieren enormemente en afinidad taxonómica, hábitos de vuelo, tamaño y forma.

[Traducción del equipo editorial]

Species with wide distributions are often exposed to a variety of environmental conditions that may result in a number of populations having unique morphologies that reflect local conditions. Evolutionary responses to natural selection associated with environmental variation may consist of population-level genetic divergence or phenotypic plasticity (James 1983, 1991, Via and Lande 1985,

Bull 1987). Studies of geographic variation in avian populations have documented differences in body size, wing length, leg and foot shape, and bill size and shape that have been correlated with variation in climate, habitat, or ecology (e.g., James 1970, 1991, Wattel 1973, Leisler et al. 1989, Whaley and White 1994, Fitzpatrick and Dunk 1999).

In this study, we examine geographic variation of morphology within four species of migratory raptors to determine the degree to which different species exhibit concordant patterns. If there is geographic variation in morphology, it might be attributed to environmental conditions in breeding or wintering habitat. James (1991) found that birds

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from cool, dry climates tend to be large while those from warm, humid climates tend to be small as predicted by Bergmann's rule. Alternatively, migration patterns and habits may influence morphology and be exhibited in wing and tail characteristics relative to body size.

Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperii*), Red-tailed Hawks (*Buteo jamaicensis*), and American Kestrels (*Falco sparverius*) are all found throughout North America with many populations exhibiting seasonal north-south migration. Individuals were sampled from two migratory routes in western North America and one on the east coast. While little can be said about the breeding grounds for birds captured on migration, some hypotheses can be developed regarding migratory patterns and some general statements about potential adaptations to wintering and breeding habitat can be made.

The Goshute Mountains of Nevada and the Manzano Mountains of New Mexico are monitoring points along major raptor flyways in the west (Hoffman et al. 2002), and Cape May Point in New Jersey is situated on a major eastern flyway (Clark 1985). The Goshute and Manzano mountain flyways are both situated along mountainous-ridge systems. Migrants through Cape May Point build up along the Atlantic coastline and funnel into the southern New Jersey peninsula to cross the Delaware Bay. Based on available band returns, breeding grounds are thought to be north of the western flyways (Smith et al. 1990, Hoffman et al. 2002), and north and east of the eastern flyway (Clark 1985, W. Clark pers. comm.). Goshute and Manzano migrants travel each fall to wintering grounds in central and western Mexico, a distance that may be as much as twice that of eastern migrants, which tend to remain in the southeastern United States (Clark 1985, Smith et al. 1990, W. Clark pers. comm.). The wintering grounds of raptors provide important habitat for a substantial portion of the year.

Consistent variation in morphology across taxa is supportive of the idea that ecological or environmental factors may drive such patterns. The single flight-related activity that all these species have in common (western vs. eastern populations) is their migratory pattern. With flights through the Manzanos and Goshutes occurring in high-altitude-arid mountains and continuing for longer distances, greater flight surfaces may decrease wing loading, and hence may increase flight efficiency in these

habitats. A habitat-related variable on both breeding and wintering grounds that might influence body size would be climate. However, we were unable to make specific predictions with regards climate and body size without additional information as to the origin and destination of the birds.

METHODS

Morphological Variables. Between September and November 1991–94 we collected mensural information from raptors trapped while in migration on each of three flyways. We measured mass, length of central rectrix (Tail), wing chord (Wing), tarsus length (Tarsus Length), tarsus width at the narrowest point (Tarsus Width), culmen length (Culmen; bill from cere to tip) and hallux length (Hallux; length of hind claw) using a balance, dial calipers, metric ruler, and wing-chord ruler. In the absence of wing and tail surface area measurements, wing and tail length were taken to be indicators of flight-surface area. Flight-surface area is a function of length and width, and wing area increases proportionally as a square of wing span in wings of similar shape (Tucker and Parrott 1970, Pennycuik 1975). Any birds with a noticeable crop were removed from analyses involving body mass. Sharp-shinned Hawks, Cooper's Hawks, and American Kestrels were grouped according to gender and age because of sexual dimorphism and differential growth of feathers. Red-tailed Hawks were grouped only by age. Results are reported for hatch-year birds only; samples of adult birds were too small for statistical analyses.

We log-transformed all measurements to conform to a multivariate-normal distribution and compared character by character using StatGraphics (Manguistics, Inc., Rockville, MD U.S.A.) multiple analysis of variance. We also performed multivariate analyses to remove possible allometric relationships and to investigate morphological shape variables. Principal component scores were determined for each species and gender, after which scores were assigned to individuals. For the principal components analysis, mass was eliminated from analyses of size and shape because it was highly variable and may have simply reflected the physical condition of migrants. We used analysis of variance to test for significant differences between flyways for each component score. Correlation analysis of the first three principal components and the morphological measurements was also performed.

RESULTS

Univariate Analyses. With the exception of marginal pattern in the female Sharp-shinned Hawk, all four species of raptor and both genders were significantly heavier in the east than in the west (Tables 1–4). Sharp-shinned Hawks averaged 5% heavier in the east than in the west, American Kestrels were 7% (males) and 9% (females) heavier in Cape May than in the west, Red-tailed Hawks were about 17% heavier in the east than in the west, and Cooper's Hawks showed the greatest difference at 23% (males) and 29% (females) heavier in the east

Table 1. Results of multiple analysis of variance for significant differences in mean morphological characters of male and female hatch-year Sharp-shinned Hawks in three flyways. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was given in grams and linear measurements in millimeters. Values for males are in the first line, females in the second.

CHARACTER	GOSHUTES	MANZANOS	CAPE MAY	P-VALUE
MALES	N = 100	N = 21	N = 24	
FEMALES	N = 87	N = 9	N = 37	
Mass	98.3 (6.3) ^a	98.4 (7.1) ^a	102.9 (7.1) ^b	0.009
	162.9 (12.2) ^a	170.1 (15.5) ^{ab}	170.5 (15.6) ^b	0.016
Tail	138.4 (3.0) ^a	139.3 (3.5) ^a	131.5 (4.9) ^b	<0.001
	162.7 (5.0) ^a	160.0 (6.3) ^a	154.1 (5.4) ^b	<0.001
Wing	170.7 (2.9) ^a	172.3 (2.7) ^b	164.8 (4.2) ^c	<0.001
	202.2 (4.1) ^a	202.4 (4.5) ^a	195.6 (4.7) ^b	<0.001
Tarsus length	50.4 (1.2) ^a	49.6 (1.0) ^b	48.7 (1.8) ^c	<0.001
	56.3 (1.4) ^a	54.8 (1.9) ^b	55.2 (1.6) ^b	<0.001
Tarsus width	3.4 (0.2) ^a	3.6 (0.1) ^b	3.5 (0.2) ^b	0.001
	4.3 (0.3) ^a	4.4 (0.3) ^{ab}	4.5 (0.3) ^b	0.003
Hallux	11.4 (0.4) ^a	11.4 (0.4) ^a	11.1 (0.5) ^b	0.001
	14.3 (0.5) ^a	14.3 (0.6) ^a	14.3 (0.6) ^a	0.944
Culmen	9.8 (0.3) ^a	9.7 (0.4) ^a	10.0 (0.4) ^b	0.006
	11.9 (0.4) ^a	11.9 (0.3) ^a	12.2 (0.5) ^b	<0.001

than in the west. Three species had significantly longer mean wing and tail length in the west than in the east, with the exception of the Cooper's Hawk.

Leg length and width also varied between flyways. There was a tendency for raptors migrating

through the Goshute Mountains to have longer and/or thinner tarsi than other migrants but the pattern was not significant for all species. Culmen length was longest in Cape May for Sharp-shinned Hawks, female Cooper's Hawks and Red-tailed Hawks.

Table 2. Results of analysis of variance for significant difference in morphological characters between flyways for male and female hatch-year Cooper's Hawks. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was measured in grams and linear measurements in millimeters. Values for males are in the first line, females in the second.

CHARACTER	GOSHUTES	MANZANOS	CAPE MAY	P-VALUE
MALES	N = 37	N = 36	N = 37	
FEMALES	N = 28	N = 39	N = 21	
Mass	253.7 (15.5) ^a	266.6 (26.0) ^a	339.2 (38.7) ^b	<0.001
	378.5 (25.9) ^a	400.5 (35.5) ^b	530.3 (41.0) ^c	<0.001
Tail	188.8 (6.4) ^a	194.3 (5.1) ^b	191.0 (5.6) ^a	<0.001
	214.1 (8.1) ^a	217.2 (6.6) ^a	216.9 (7.8) ^a	0.254
Wing	220.1 (4.8) ^a	226.0 (5.0) ^b	228.0 (4.9) ^c	<0.001
	251.5 (4.8) ^a	255.2 (5.9) ^b	260.1 (6.7) ^c	<0.001
Tarsus length	62.2 (1.9) ^a	61.7 (1.6) ^a	65.0 (1.8) ^b	<0.001
	68.6 (2.1) ^a	67.3 (2.3) ^b	73.2 (1.8) ^c	<0.001
Tarsus width	5.4 (0.3) ^a	5.7 (0.3) ^b	6.0 (0.5) ^c	<0.001
	6.6 (0.4) ^a	7.1 (0.4) ^b	7.4 (0.5) ^c	<0.001
Hallux	18.8 (0.6) ^a	18.8 (0.6) ^a	19.7 (0.6) ^b	<0.001
	22.3 (0.8) ^a	22.2 (0.6) ^a	23.8 (1.7) ^b	<0.001
Culmen	14.7 (0.5) ^a	14.7 (1.1) ^a	14.9 (2.0) ^a	0.715
	17.2 (1.2) ^a	17.0 (1.5) ^a	19.2 (0.9) ^b	<0.001

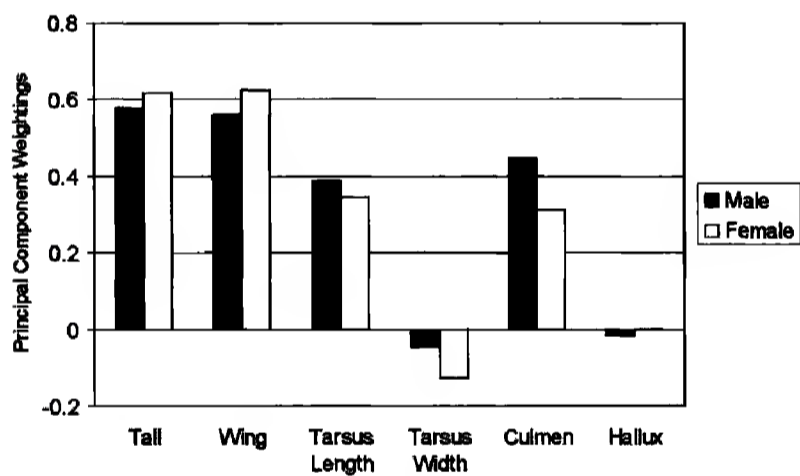
Table 3. Results of analysis of variance for significant differences in morphological characters between flyways for hatch-year Red-tailed Hawks. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was measured in grams and linear measurements in millimeters.

CHARACTER	GOSHUTES N = 152	MANZANOS N = 62	CAPE MAY N = 12	P-VALUE
Mass	933.4 (150.5) ^a	950.2 (124.3) ^a	1134.4 (143.6) ^b	<0.001
Tail	233.7 (11.3) ^a	235.8 (11.0) ^a	222.1 (9.5) ^b	<0.001
Wing	397.4 (17.2) ^a	403.6 (17.2) ^b	387.3 (14.8) ^a	0.004
Tarsus length	87.7 (4.2) ^a	88.5 (4.2) ^a	85.8 (9.0) ^a	0.145
Tarsus width	10.8 (0.9) ^a	11.0 (0.8) ^a	12.8 (0.7) ^b	<0.001
Hallux	28.8 (2.0) ^a	29.2 (1.6) ^a	32.6 (2.2) ^b	<0.001
Culmen	25.1 (1.4) ^a	25.1 (1.4) ^a	28.1 (1.4) ^b	<0.001

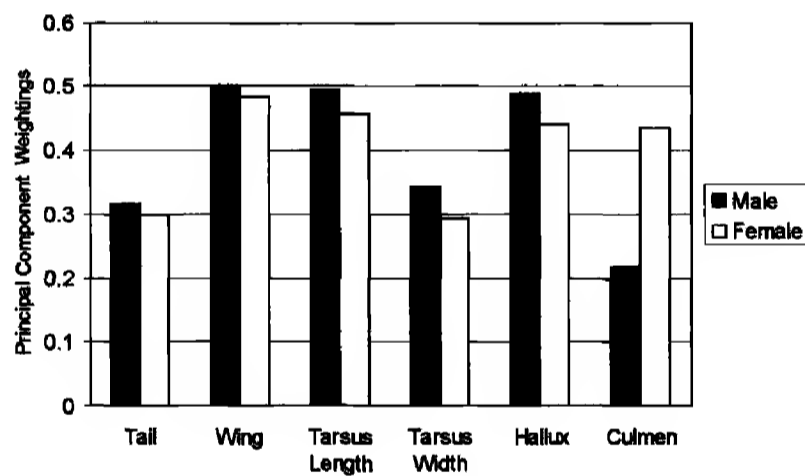
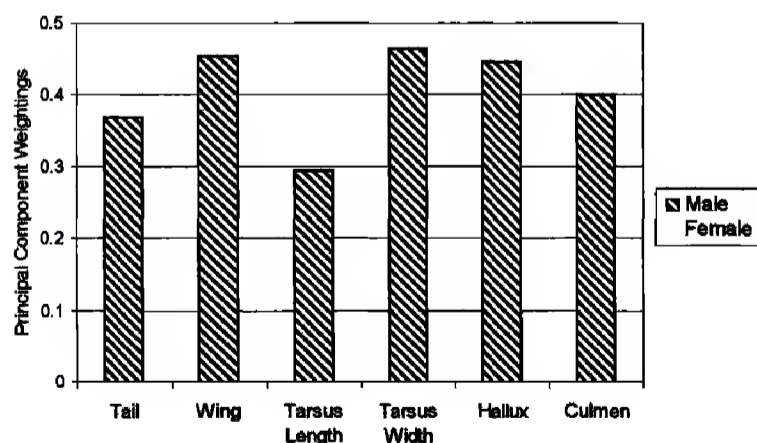
Multivariate Analyses. The first principal component (PC1) was interpreted as an overall size component in the Cooper's Hawk and Red-tailed Hawk (Fig. 1). This component explained 37% and 45% of the variation in male and female Cooper's Hawks, respectively, and 59% of the variation in Red-tailed Hawks. Weightings (Manly 1994) of all the characters were, generally, equally high. Val-

ues of PC1 were highest for wing and tail, with values for other characters being lower, in the Sharp-shinned Hawk and in the American Kestrel (Fig. 1). This component explained 32% and 33% of the variation in male and female Sharp-shinned Hawks, and 27% and 29% of the variation in male and female American Kestrels.

Individuals of all four species were significantly



Sharp-shinned Hawk



Cooper's Hawk

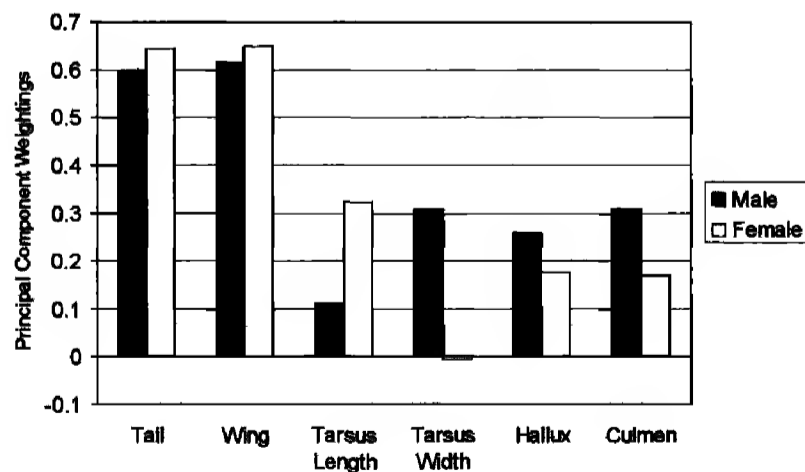


Figure 1. Principal component weightings (PC1) for six morphological variables (Tail = tail length, Wing = wing length, tarsus length, tarsus width, Hallux = hallux length, and Culmen = culmen length) are presented as bar graphs. Genders could not be distinguished in Red-tailed Hawks.

Table 4. Results of analysis of variance for significant differences in morphological characters between flyways for male and female hatch-year American Kestrels. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was measured in grams, linear measurements are in millimeters. Values for males are in the first line, females in the second.

CHARACTER	GOSHUTES	MANZANOS	CAPE MAY	P-VALUE
MALES	<i>N</i> = 205	<i>N</i> = 21	<i>N</i> = 14	
FEMALES	<i>N</i> = 158	<i>N</i> = 13	<i>N</i> = 13	
Mass	100.9 (7.9) ^a	102.5 (7.6) ^a	109.6 (10.2) ^b	0.001
	107.6 (9.1) ^a	114.1 (9.7) ^b	121.7 (7.5) ^c	<0.001
Tail	121.9 (4.9) ^a	121.1 (6.2) ^a	116.4 (4.5) ^b	0.0001
	126.6 (5.3) ^a	124.5 (7.3) ^{ab}	121.8 (3.3) ^b	0.005
Wing	188.7 (5.6) ^a	191.6 (5.3) ^b	180.1 (5.5) ^c	<0.001
	197.1 (6.1) ^a	196.7 (8.5) ^a	191.2 (5.7) ^b	0.005
Tarsus length	36.4 (2.1) ^a	35.6 (1.6) ^b	35.5 (2.5) ^{ab}	0.050
	36.3 (1.9) ^a	35.6 (2.0) ^a	35.4 (1.7) ^a	0.152
Tarsus width	4.1 (0.3) ^a	4.1 (0.4) ^a	3.8 (0.2) ^b	0.011
	4.2 (0.4) ^a	4.4 (0.4) ^b	4.3 (0.4) ^{ab}	0.083
Hallux	9.4 (0.5) ^a	9.8 (0.7) ^a	9.5 (0.5) ^a	0.704
	9.8 (0.7) ^a	9.7 (0.5) ^a	9.8 (0.4) ^a	0.954
Culmen	11.6 (0.6) ^a	11.6 (0.7) ^a	11.8 (0.8) ^a	0.254
	11.9 (0.7) ^a	12.3 (0.6) ^a	12.2 (0.5) ^a	0.083

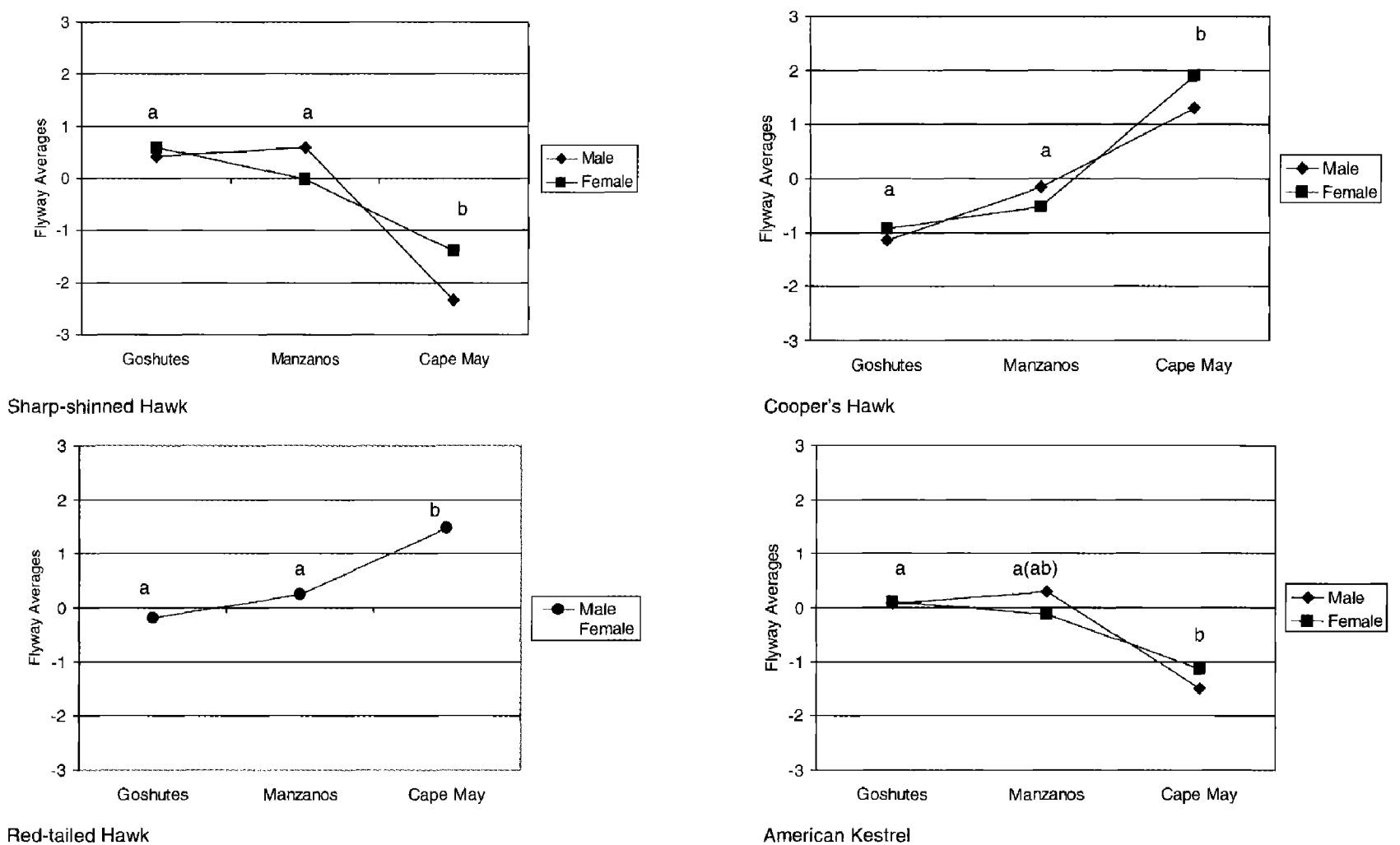


Figure 2. Principal component 1 scores (y-axis) were assigned to individuals and significant differences between flyways were determined by analysis of variance. Significantly different means ($P < 0.05$) for flyways (Goshute Mountains, Manzano Mountains, and Cape May Point) are indicated by unique letters. Genders could not be distinguished in Red-tailed Hawks.

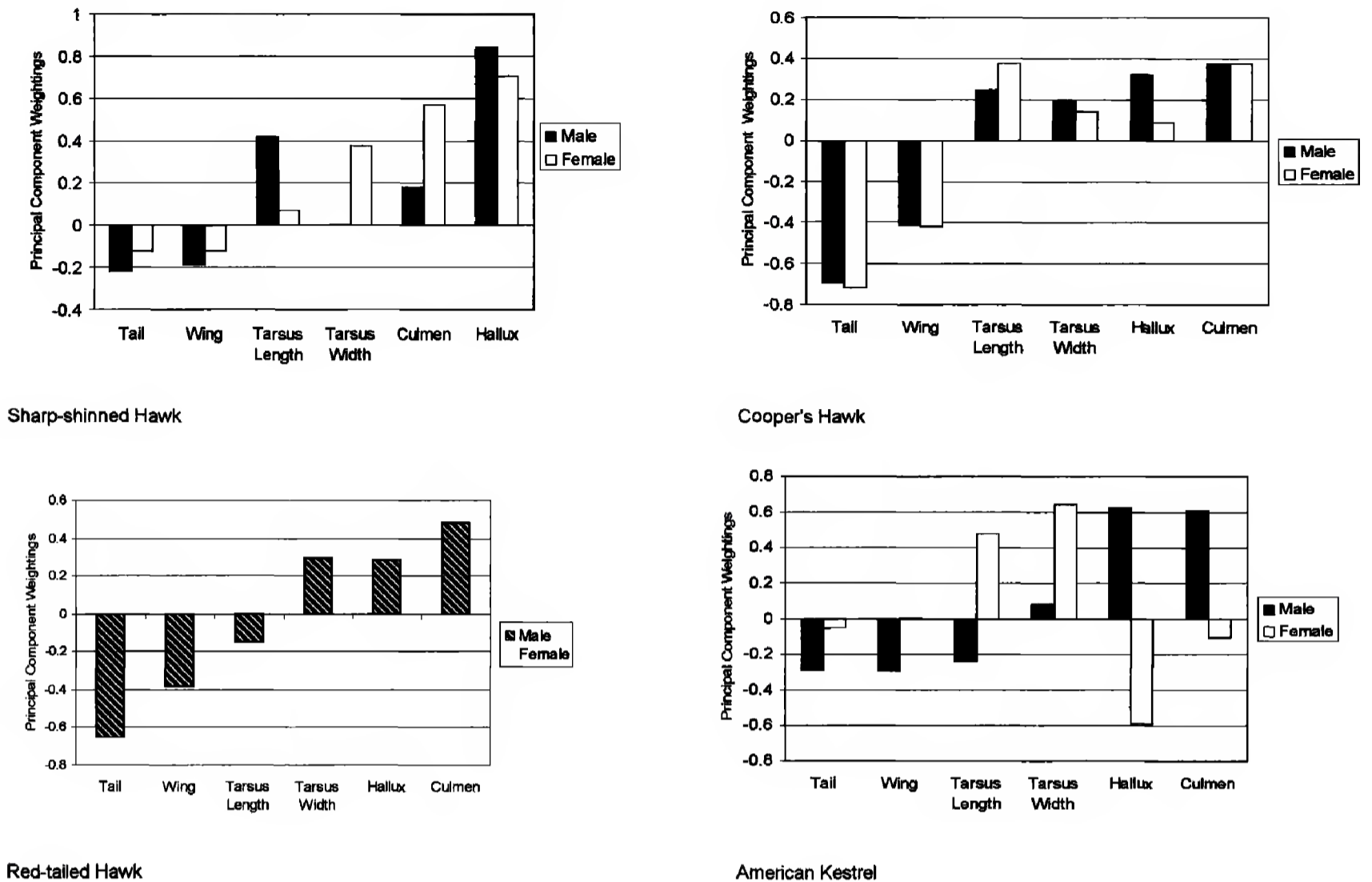


Figure 3. Principal component weightings (PC2) for six morphological variables (Tail = tail length, Wing = wing length, tarsus length, tarsus width, Hallux = hallux length, and Culmen = culmen length) are presented as bar graphs. Genders could not be distinguished in Red-tailed Hawks.

different for mean PC1 scores between eastern and western flyways except for female American Kestrels, which were significantly different only between Goshute Mountains and Cape May Point (Fig. 2). The general pattern indicated large overall size in eastern Cooper's Hawk and Red-tailed Hawk migrants, and long mean wings and tail in western Sharp-shinned Hawks and American Kestrels.

PC2 was interpreted to be a shape component in Cooper's and Red-tailed hawks (Fig. 3). Tail and wing loaded opposite to other characters. Cooper's Hawks migrating through the Manzano Mountains were significantly different for mean PC2 scores from those migrating through the other flyways and had longer tails than Goshute and Cape May migrants (Table 2, Fig. 4). This component explained 19% and 20% of the variation in male and female Cooper's Hawks, and 13% of the variation in Red-tailed Hawks. Red-tailed Hawks migrating through Cape May Point were significantly different from the other flyways for this component and

had shorter wings and tail than western migrants (Table 3, Fig. 3). On the other hand, PC2 consisted of variable weightings of culmen, hallux, and leg characters in Sharp-shinned Hawks and American Kestrels (Fig. 3). PC2 explained 19% and 20% of the variation in male and female Sharp-shinned Hawks, and 18% of the variation in both sexes of the American Kestrel. Although there were significant differences between some flyways (Fig. 4), variation for this component was difficult to interpret in the smaller raptors.

DISCUSSION

Four species exhibited considerable variation in size, taxonomy, predatory habits, and flight styles, yet we found a common pattern of morphological variation. The four species of raptors exhibited geographic variation in morphology among migratory flyway pathways. We were unable to correlate variation in body size with climate due to uncertainty of specific geographic location of either breeding or migratory habitat. The morphological

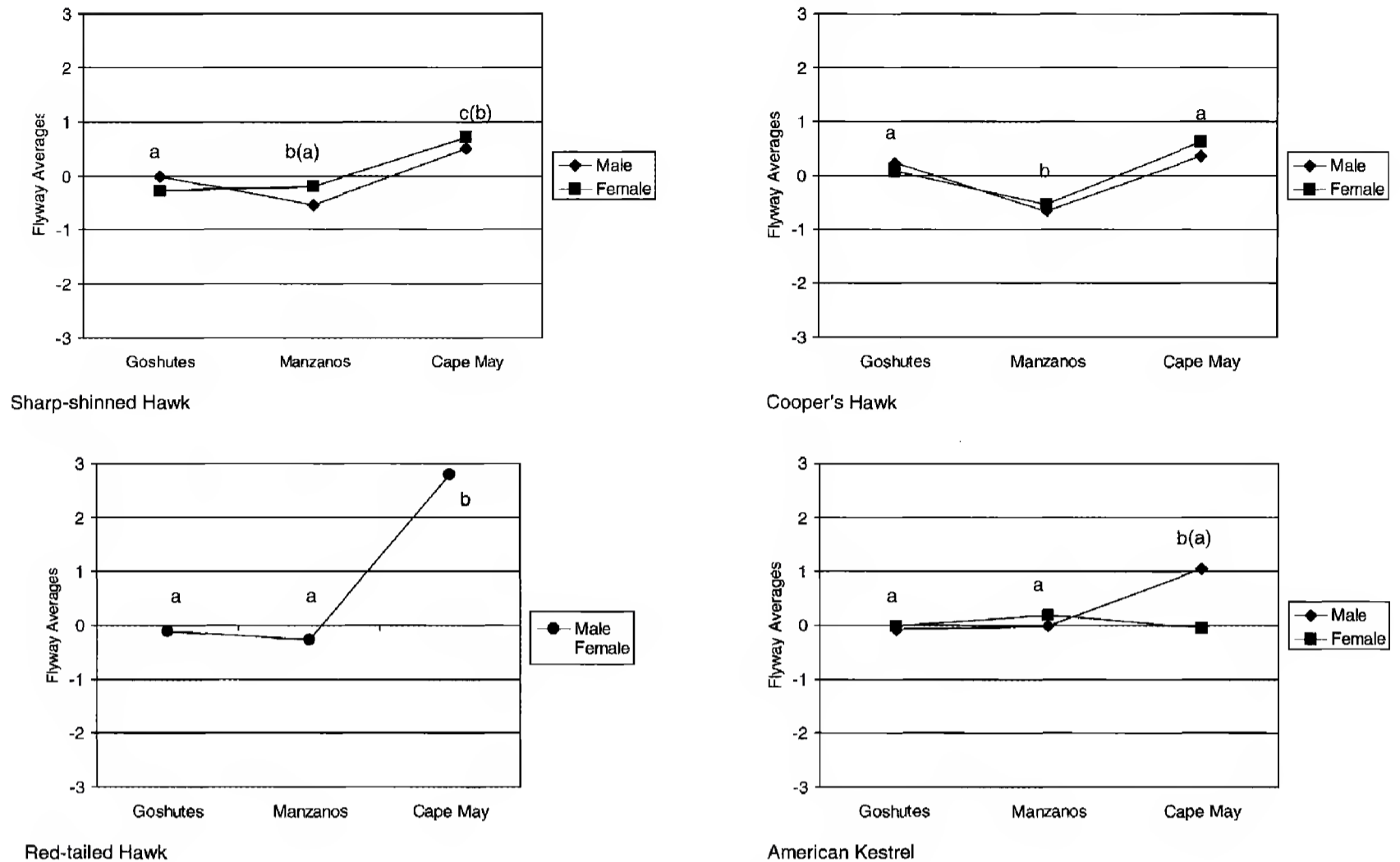


Figure 4. Principal component 2 scores (y-axis) were assigned to individuals and significant differences between flyways were determined by analysis of variance. Significantly different means ($P < 0.05$) for flyways (Goshute Mountains, Manzano Mountains, and Cape May Point) are indicated by unique letters. Genders could not be distinguished in Red-tailed Hawks.

patterns observed could result from either genetic differentiation for the traits or from phenotypic plasticity (James 1983). Of the four species in this study, only the Red-tailed Hawk consists of a number of subspecies or races in North America in the area of the study (Preston and Beane 1993). In a separate study using mitochondrial DNA (mtDNA) from the same individuals, only the Red-tailed Hawk exhibited genetic differences between eastern and western flyways indicating population genetic structure (Pearlstine 2004).

Morphological Variation and Migration Distance. The Sharp-shinned Hawk, Red-tailed Hawk, and American Kestrel exhibited variation in body mass, wing chord, and tail length consistently among the migratory flyways, whereas the Cooper's Hawk did not. Although wing area was not measured, we used wing length as an approximate indication of relative wing area within a species. Increased wing length in western raptors may result in greater wing area, thus reducing wing loading, and perhaps the cost of migratory flight. In contrast to the

raptors in this study, migratory populations of passerines do not have longer wings but they are more pointed than nonmigratory populations (Mulvihill and Chandler 1991, Senar et al. 1994, Monkkonen 1995). There is a difference in flight strategy, however, as small birds migrate primarily through flapping flight, whereas raptors tend to utilize gliding and soaring strategies to minimize flight costs (Kerlinger 1989, Alerstam 1990).

The tail is also a vital component of flight surface in birds, especially when lift is important (Thomas and Balmford 1995). Raptors can reduce wing loading by from 19.7% (Red-tailed Hawks) to 29.3% (Sharp-shinned Hawks) by simply spreading the tail (Kerlinger 1989). Despite the smaller body mass of western migrants, wings and tail were significantly longer in Sharp-shinned and Red-tailed hawks relative to Cape May migrants. Wings and tail were significantly longer in male American Kestrels from the west than from the east and wings were significantly longer in western female American Kestrels than eastern. Parallel variation be-

tween the three species from three flyways suggests possible natural selection relative to migration.

Morphological Variation and Climate. Variation in body mass among the three flyways revealed consistently larger body size in the east than in the west. Mean mass for all species was greater in the east, and PCI in the large raptors supports the observation of relatively large eastern individuals for Cooper's and Red-tailed hawks. Other studies of geographic variation correlated with climate have provided support for Bergmann's rule, though not for the same geographic areas as this study (James 1970, Aldrich 1984, Murphy 1985, Aldrich and James 1991). A comprehensive review of avian morphology by Zink and Remsen (1986) however, revealed that only 42% of studies provide unambiguous evidence of correlation between body size and climate. One study of Red-tailed Hawks also failed to support variation in body size according to Bergmann's rule (Fitzpatrick and Dunk 1999). Additionally, predictions from Bergmann's rule have not been supported for migratory species. The variation in body size revealed by this study was consistent with results of Zink and Remsen's (1986) analysis. Bergmann's rule may hold true however, for body size comparisons made with respect to wintering habitat (e.g., Johnston and Fleischer 1981, Wiedenfeld 1991). Clearly, raptors must be studied on both wintering and breeding grounds to further understand this pattern.

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